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RESEARCH ARTICLE

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Bimanual coordination between isometric contractions and rhythmic movements: an asymmetric coupling

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Abstract Interactions between rhythmically moving limbs typically result in attraction to a limited number of coordination modes, which are distinguished in terms of their stability. In addition, the stability of coordination typically decreases with elevations in movement frequency. To gain more insight into the neurophysiological mechanisms underlying these stability characteristics, the effects of phasic voluntary muscle activation onto the movement pattern of the contralateral limb as well as onto the stability of interlimb coordination were examined. This was done in circumstances in which a minimal degree of movement-elicited afferent information was available to mediate the coupling influences. The task involved rhythmic application of isometric torque by one hand, while the other hand was moving rhythmically with unconstrained amplitude. The effects of two levels of applied torque, two coordination patterns (inphase and antiphase), and two movement frequencies were determined, both at the behavioural level (movement kinematics and kinetics) and the neuromuscular level (EMG). The isometric applications of torque clearly influenced the muscle-activation profile and movement pattern of the other limb, affecting both temporal variability and amplitude. Surprisingly, there were no differences between the two coordination patterns or between the tempo conditions. As such, the results did not conform to the Haken-Kelso-Bunz model for rhythmic movement coordination. These data suggest that the archetypal differences in stability of rhythmic bimanual coordination are contingent upon a correspondence between the limbs in terms of their respective tasks. This interpretation is elaborated in terms of the role of sensory feedback and the functional specificity of motor unit recruitment in rhythmic interlimb coordination.

Key words Rhythmic movements · Coordination dynamics · Stability · Electromyography · Isometric

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Introduction

Bimanual coordination is characterised by interactions between the limbs (e.g. Kelso et al. 1979; Marteniuk et al. 1984; Von Holst 1938). As a consequence of these (mutual) influences, the resulting behaviour is attracted to a limited number of stable coordination patterns. For isochronous rhythmic coordination between two limbs, for instance, only the inphase (simultaneous movement in the same direction, resulting in a phase differences of 0°) and antiphase pattern (simultaneous movements in opposite directions, resulting in a phase difference of 180°) can be maintained in a stable fashion without specific training (e.g. Tuller and Kelso 1989; Zanone and Kelso 1992). Although both patterns can be performed, the inphase pattern is more easily generated than the antiphase pattern (e.g. Baldissera et al. 1982; Cohen 1971). It has been demonstrated convincingly that this difference in the ease of performance results from the differential stability of these two modes of coordination, with the antiphase pattern being less stable than the inphase pattern. In addition, it has been shown that the stability of the two coordination patterns is inversely related to the frequency of the movements: When starting in the antiphase coordination, a gradual increase in movement frequency induces a sudden unintended transition to the inphase coordination mode (e.g. Kelso 1984; Kelso et al. 1987).

The empirically identified stability characteristics of isochronous interlimb coordination have been mathematically modelled by means of a potential function that de-

scribes the observed dynamics of relative phase (i.e. the phase difference between the two moving limbs; Haken et al. 1985). This dynamical model was formulated in abstract terms, without reference to the structural properties of the moving (oscillating) components or the way in which they interact. As a result, the Haken-Kelso-Bunz (or HKB) model could be generalised to a variety of situations, including coordination between different effector systems (e.g. an arm and a leg; Carson et al. 1995; Jeka and Kelso 1995), between a single limb and environmental stimuli (Byblow et al. 1995; Kelso et al. 1990; Wimmers et al. 1992), and even between two different persons (Amazeen et al. 1995; Schmidt et al. 1990). The fact that the behaviour of systems with rather different structural properties, with respect to both the oscillating components and the way in which they interact, are characterised by the same stability-related phenomena underscores the relevance of modelling the system's dynamics at an abstract level of analysis.

Although the principles of coordination appear to be more general than the systems in which they are embodied, in each specific case the coordination between the moving components has to be instantiated in a neural-muscular substrate. In the search for an understanding of rhythmic interlimb coordination more in terms of the structural properties of the movement system, a point of departure may be found in the empirically demonstrated variations in stability and the way that these are accounted for by dynamical models (Peper and Beek 1998a; Peper and Beek, 1999). At the same time, knowledge about the neurophysiological mechanisms involved in stability-related coordination phenomena might guide the derivation and further elaboration of such models.

Neurophysiological bases of interlimb interaction

Several studies suggest that afferent feedback arising from movement assumes an important role in determining the stability of rhythmic interlimb coordination in humans. It has been demonstrated that the passive movement of one limb entrains the phase and frequency of the contralateral limb (deGuzman and Kelso 1991; Gunkel 1962). In addition, experimenter-induced movement of a third limb produces disruption of the coordination between two actively moving limbs (Swinnen et al. 1995). On the basis of adaptations to elastic and inertial loads, Baldissera et al. (1991) argued that peripheral signals have an entraining influence, supporting the inphase coordination between the limbs. It was proposed that central "inhibitory action" may be necessary in order to prevent such entrainment.

The influence of peripheral signals, arising from movement, upon the stability of interlimb coordination may be a consequence of the modulations of the excitability of spinal pathways, which have been demonstrated in a variety of rhythmic movement tasks. Inhibition of the H-reflex, for example, is minimal during the phases of movement in which the target muscle is active, and maximal during the phases in which it is inactive (e.g. Brooke et al. 1992; Brooke et al. 1995). Yet, the degree of modulation is not simply dependent upon the level of muscle activation required to drive the limb (e.g. Brown and Kukulka 1993; Capaday and Stein 1986; Capaday and Stein 1987; Crenna and Frigo 1987). Rather, it appears to be attributable to "movement-elicited afference" (McIlroy et al. 1992) that is mediated primarily by muscle spindles rather than by cutaneous, joint, or pressure receptors (Burke et al. 1984; Cheng et al. 1995). The degree of inhibition is elevated with increasing velocity of movement (McIlroy et al. 1992), and restriction of movement attenuates markedly the extent of the reflex modulation (e.g. Romanò and Schieppati 1987).

Recent findings emphasise that in addition to being contingent on the joint angle of the target limb (Brooke et al. 1992), the magnitude of the H-reflex is also dependent on the position and frequency of movement of the contralateral limb (Carson et al. 1999; McIlroy et al. 1992). Although significant modulation of reflex gain appears to require relatively large ranges of motion and angular velocities of the joints (Brooke et al. 1995), the receptor discharge that arises from even passive rotation of a limb exerts a strong influence upon the reflex pathways on the opposite side. The extent of this contralateral modulation is in turn increased with the velocity of passive rotation (Collins et al. 1993), and appears to be related directly to the rate of change of length of the muscles of the moving limb (Cheng et al. 1995). However, whereas this crossed inhibition is dependent on the movement phase of the other limb when it is actively moving, no such phase dependency is observed when the inhibition is induced by passive motion of the contralateral limb (Cheng et al. 1998). The evidence available at present suggests that the modulation is accounted for largely by presynaptic inhibitory mechanisms (see Brooke et al. 1997; Stein 1995). These findings suggest a possible means by which afferent feedback, arising from specific elements of the somatosensory receptor array during movement, may promote the entrainment of the limbs (Hasan et al. 1985).

In the context of locomotion, movement-induced modulation of reflex gain is highly adaptive. In particular, the regulation of reflex pathways innervating soleus may serve to ensure that the gain is high during stance, and reduced when the amplitude of leg movement is increased following the initiation of the step cycle. The contralateral component to such modulation has been attributed to the redundancy that is characteristic of the mammalian nervous system (Brooke et al. 1997). In spite of the phylogenetic separation of function of the upper and lower limbs, a similar phase-dependent modulation of spinal reflex responses can be observed in the wrist flexor (flexor carpi radialis) during rhythmic flexion-extension movements of the ipsilateral foot (Baldissera et al. 1998) and during movement of the contralateral wrist (Carson et al. 1999). The presence of pathways in the upper limb that mediate crossed inhibition suggests the specific means by which afferent feedback, arising from

movement-elicited discharge of somatosensory receptors, may mediate interactions between the limbs during bimanual coordination.

Despite the demonstrated role of movement-related afferent feedback in mediating interactions between the limbs, the question remains whether such feedback is essential in generating the prototypical characteristics of interlimb coordination. It has been proposed previously that the loss of stability of asynchronous modes of coordination may be due to an inefficacy of the central specification of muscle activation patterns (Carson 1995). Studies with deafferented patients (e.g. Teasdale et al. 1994) indicated that interactions between the limbs are also observed in the absence of movement-elicited afferent information. In addition, a clear coupling between a phantom limb and the contralateral limb has been demonstrated in an amputee with subjective experience of movement of the phantom limb (Franz and Ramachandran 1998).

A possible explanation for the interactions between the limbs that are observed in the absence of afferent feedback, may be found in empirically demonstrated bilateral effects of central activation. Lack of independence in the most distal musculature has been ascribed to a divergence of corticomotoneuronal projections to functionally related motoneurone pools (Buys et al. 1986; Cheney and Fetz 1985). It has been suggested that patients with overt mirror movements (e.g. Farmer et al. 1989) represent an extreme end of a spectrum of contralateral activation due to bilateral projections, that is expressed in varying degrees in all individuals (Chiappa et al. 1991). Recent studies have demonstrated that responses evoked in the musculature of the hand, by transcranial magnetic stimulation (TMS) of the motor cortex, are facilitated by tonic contraction of homologous muscles of the contralateral limb (Hess et al. 1986; Hess et al. 1987). Such crossed facilitation could be mediated by intracortical excitation or at the spinal cord level. As it has also been observed in an amputee performing "contractions" of the phantom hand, it is unlikely to be mediated by afferent input from the limb (Hess et al. 1986). In addition, several studies have revealed that, in monkeys, in the primary motor cortex (Aizawa et al. 1990; Matsunami and Hamada 1981), the supplementary motor area (Brinkman and Porter 1979; Tanji et al. 1988), and the premotor cortex (Gentilucci et al. 1988) a number of neurones are specifically engaged in the production of bilateral movements (see also Wiesendanger et al. 1994). It remains to be established whether, during interlimb coordination, these cells exhibit firing patterns that are related to the phase relations between the limbs.

In a recent investigation, Carson et al. (1999) demonstrated that during rhythmic voluntary oscillations about the left wrist, motor-evoked potentials recorded from the (quiescent) muscles of the right forearm were potentiated relative to resting control conditions. Furthermore, the magnitudes of the evoked responses were modulated strongly during the cycle of movement of the contralateral (left) hand. In particular, the responses were larger during the movement phases that involved activation of the homologous muscles in the left forearm. In contrast, during passive movements of the left wrist, both H-reflex responses and motor-evoked potentials, recorded from the muscles of the right forearm, were inhibited relative to resting control conditions. These data suggest that the phase-dependent potentiation of the corticospinal volley, that resulted from active movement of the opposite limb, was not simply mediated by afferent feedback arising from the movement. Rather, the potentiation appears to be brought about by a contralateral component of the descending input to the spinal cord. Given the phase dependency of the potentiation, it is possible that it may have a disruptive influence on the stability of asynchronous patterns of interlimb coordination.

Neurophysiological aspects of pattern stability?

In sum, there are a number of neurophysiological mechanisms that may mediate interactions between the limbs during rhythmic coordination. The question remains, however, as to which of these are essential in generating the observed stability characteristics? This issue is underscored by a recent demonstration that the relative stability of the inphase and antiphase modes of coordination is preserved in isometric bimanual contractions (Carson 1995). During isometric contractions, the integration of sensory information from peripheral receptors is likely to be quite different from that which occurs when contractions are accompanied by substantial changes in muscle length. Golgi tendon organs are thought to assume an important role in signalling variations in contractile force (e.g. Rothwell 1994), and cutaneous, joint, and pressure receptors may also provide information during contractions of this kind. It is likely however, that during isometric contractions, discharge from the primary stretch receptors of the muscle spindles is quite different from that which occurs during shortening contractions. The differential stability of the inphase and antiphase modes of coordination, and the associated observation that pattern stability decreased with increases in movement frequency, seem to suggest that these stability-related phenomena do not depend critically on afferent signals arising from displacement of the limbs.[1]

The correspondence between the results obtained for the coordination between isometric contractions and those typically observed for rhythmically moving limbs may indicate that also in the latter situation movement-elicited sensory information is not essential in establishing the usual stability characteristics. This possibility was addressed in the present experiment, which examined the manner in which phasic voluntary muscle activation affects the movement pattern of the contralateral

[1] In Carson's (1995) study no frequency-induced transitions from antiphase to inphase coordination were observed. This may suggest that the integration of movement-derived sensory feedback plays an important role in inducing such transitions (cf. Baldissera et al. 1991).

limb in circumstances in which a minimal degree of movement-dependent afferent information is available to mediate such interactions. This was achieved in the context of an asymmetric task, in which one hand performed isometric contractions, while the other hand moved rhythmically with unconstrained amplitude. Cohen (1970) demonstrated that the rapid application of an isometric wrist flexion torque has a marked influence on alternating movements of the contralateral limb. This effect was similar to that resulting from an active (flexion) displacement about the wrist. The present experiment focused on possible coupling effects resulting from *rhythmic* isometric contractions applied by one hand, on the patterns of movement generated by the contralateral hand, and on the stability of coordination between the hands. As there was essentially no displacement of the "isometric hand", it was unlikely that its influence on the "dynamic hand" could be mediated by the integration of movement-dependent afferent feedback.

The purposes of the experiment were mainly exploratory. In order to examine the effect of the level of muscle activation on the movement pattern of the opposite limb, participants were required to generate two distinct levels of isometric torque. We also examined both inphase and antiphase patterns of coordination. Given the correspondence between Carson's (1995) results and the predictions of the HKB model, it was anticipated that the antiphase coordination pattern would be less stable than the inphase pattern. In addition, by having participants perform at two different frequencies, we were able to examine whether, in line with the HKB model and the empirical results of Carson (1995), pattern stability was affected by the tempo of performance. Although this manipulation was not expected to result in unintended transitions from antiphase to inphase coordination, the stability of performance of both coordination patterns was predicted to be lower at the higher frequency of performance (cf. Haken et al. 1985; Sternad et al. 1995). Both movement kinematics and joint kinetics [frequency and amplitude and their coefficients of variation (CV)] and electromyographic (EMG) activity [variability in timing of the onsets of EMG bursts in flexor carpi radialis (FCR) and extensor carpi radialis (ECR) as well as the amplitudes of the EMG] were examined. As the study focused on the coupling between the limbs, bimanual performance was compared with unimanual control trials. Although not of primary interest, the coupling influences of the dynamic limb onto the isometric limb were also examined in this fashion. In addition, the stability of the coordination between the two limbs was determined, both at the behavioural level and at the neuromuscular level.

Materials and methods

Subjects

Six self-professed right-handed subjects (two females and four males), aged 21 to 41, volunteered to participate in this experiment. They gave informed consent to the procedures, which were approved by The University of Queensland medical ethics committee.

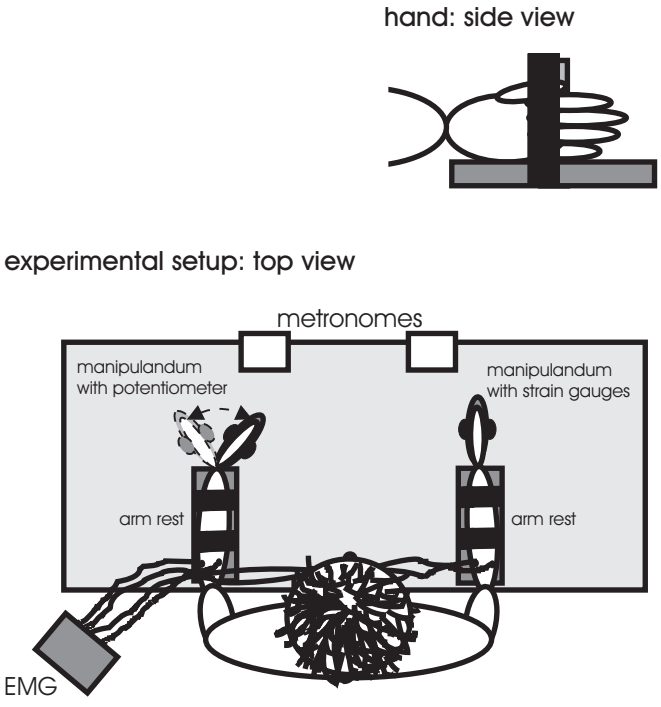

Fig. 1 Schematic representation of the experimental set-up. The positions of the manipulanda could be interchanged in order to accommodate the two left-right configurations (see text for details)

Apparatus

Subjects were seated at a table with each forearm supported and secured in a neutral position (i.e. ulnar side down) by an adjustable brace (see Fig. 1). The elbows were semi-flexed (100° to 120°). Angular displacements (dynamic hand) and torques (isometric hand), generated at the wrist, were transduced using custom built manipulanda. Shafts located coaxially with the centres of rotation of the wrists were instrumented with either strain gauges (isometric hand) or a potentiometer (dynamic hand). The hands were fixed securely to these shafts at the mid palm, obviating the activation of the long finger flexor muscles arising from formation of a grasp. During isometric contractions, the shaft was fixed in place, with the wrist in a neutral position. Thus, torques were transmitted to the manipulandum via the palmar and dorsal surfaces of the hand. Periodic auditory pacing signals (two per movement cycle) were presented via two loudspeakers positioned in front of the subjects. These signals [50 ms square waves (500 Hz and 1000 Hz)] were generated by a custom I/O board mounted in a microcomputer.

Electromyographic recordings

The EMG activity of the flexor carpi radialis (FCR) and extensor carpi radialis (ECR) muscles was recorded using Ag-AgCl surface electrodes, following standard skin preparation, at locations identified by electrical stimulation as the motor points. The EMG electrodes were connected to an AC preamplifier, the output of which was fed to an AC conditioning amplifier (32 Hz to 3.2 kHz). EMG signals were digitised at an analog-to-digital interface (DataQ) at a sampling rate of 1000 Hz and stored on a microcomputer.

Maximum m-wave recordings

Maximum m-waves were elicited in FCR by stimulating the median nerve at the cubital space, and in ECR by stimulating the radial nerve in the spiral groove. Stimuli (1-ms square wave) were generated by an isolated constant-current stimulator (Grass S48) and delivered transcutaneously via a bipolar electrode. Supramaximal stimulus intensity was determined prior to each test trial by increasing the voltage until there was no further increase in twitch amplitude. During each test trial (conducted separately for each target muscle), eight stimuli were applied at random intervals during a 64-s period. Stimuli were separated on average by 8 s.

Procedure

The subjects performed isometric contractions with one hand and dynamic movements with the other hand. Possible laterality effects were avoided by counterbalancing the left-right assignation across the subjects, i.e. three subjects (one female and two males) performed isometric contractions with the left hand, whereas the other three subjects (one female and two males) used the right hand for these contractions. In performing isometric contractions, subjects were required to generate one of two different levels of force. These were defined as a comfort force level and a distinctly higher level of force that could be reliably reproduced. In performing dynamic movements, no constraints on amplitude were imposed.

The experiment comprised both unimanual and bimanual trials. During the unimanual trials, subjects were instructed to generate either rhythmic movements or isometric contractions at one of two frequencies (1.0 Hz or 1.4 Hz) prescribed by the auditory metronome, or to perform these activities at a self-selected preferred frequency. During the isometric unimanual trials, these tempo requirements were combined with either a comfort or a high level of force. Nine separate unimanual conditions (three dynamic and six isometric) were thus obtained. At the start of the experiment, three trials were performed in each of the unimanual conditions. The order of presentation of these trials was randomised. Two additional trials for each unimanual condition were performed, also in random order, at the end of the experiment, following the completion of the bimanual trials.

During the bimanual trials, subjects were required to coordinate the periodic applications of torque by the isometric hand with the movements of the dynamic hand. Eight experimental conditions were examined, consisting of all combinations of the two force levels designated for the contractions in the isometric limb (comfort and high force), two movement frequencies (1.0 Hz and 1.4 Hz), and two coordination patterns (inphase and antiphase). In the inphase mode, the peak application of torque by the isometric hand in the direction of wrist flexion was required to be coincident with the peak displacement of the dynamic hand in the direction of wrist flexion. In the antiphase mode, the peak application of torque by the isometric hand in the direction of wrist flexion was required to be coincident with the peak displacement of the dynamic hand in the direction of wrist extension, and vice versa. Five trials, presented in random order, were conducted for each condition. The duration of all experimental trials was 30 s.

Data reduction

Kinematic and kinetic recordings

Kinematic (dynamic hand) and kinetic (isometric hand) data were low-pass filtered using a second-order Butterworth dual-pass filter with a cut-off frequency of 20 Hz. The time and magnitude of the maximum (flexion) and minimum (extension) angular displacements and applications of force, during each cycle, were delineated using a custom peak-picking algorithm. Discrete estimates of frequency and of amplitude (defined as the difference between the magnitudes of adjacent maxima and minima) were thus obtained. Indices of mean frequency and mean amplitude of generated torque and/or angular displacement, as well as the corresponding CVs were calculated for all trials.

For the bimanual trials, discrete estimates of the relative phase relation (in degrees) between the peak force (isometric hand) and peak displacement (dynamic hand) in the direction of wrist flexion, were derived in the following fashion (e.g. Carson 1995):

$$RP = \left(-360 \times \frac{t_m - t_n}{t_{n+1} - t_n}\right) - (360 \times (n - m)) \quad (1)$$

where t refers to the moment in time at which a given peak was attained, and n and n+1 refer to the indices of the two peaks, as obtained for the isometric hand, between which the mth peak of the dynamic hand was situated in time.[2] The mean direction of relative phase, which is a measure of central tendency, and uniformity, which is a measure of the dispersion of relative phase, were calculated following Mardia (1972). Uniformity takes values in the range of 0 to 1, and is the directional equivalent of the inverse of the ordinary sample standard deviation. When transformed to the range of 0 to ∞ (Mardia 1972), it permits the use of tests based on standard normal theory. Whereas all inferential tests were conducted using this transformed uniformity measure, the more informative untransformed uniformity values (range 0 to 1) are presented in the text.

Electromyographic recordings

EMG time series were filtered at 500 Hz, and full-wave rectified. The EMG amplitudes obtained for each muscle in the experimental trials, were normalised with respect to the corresponding supramaximal twitch amplitudes obtained during the maximum m-wave trials. The period of each movement cycle was divided into eight phases of equal duration. The root mean squared (RMS) amplitude of the full-wave rectified EMG was calculated for each of these phases. The values obtained from all cycles within a single trial were averaged.

In order to establish the onsets and offsets of EMG bursts, a linear envelope was first created through the application of a low-pass digital filter (second-order Butterworth, dual-pass, cut-off 2 Hz). These time series were then differentiated using a fifth-order central-difference algorithm. A custom peak-picking routine was applied to the resulting "velocity" profiles in order to delineate points corresponding to the maximum and minimum rates of change of activity for each EMG burst (Carson et al. 1995). The regions defined on this basis were then used to obtain estimates of the mean amplitude and variability of background EMG activity in the original rectified EMG time series. Criterion deviations (≥3×SD) from background levels were subsequently used to define EMG-burst onsets and offsets.

Having obtained estimates of the time of onset of each EMG burst for FCR and ECR, discrete estimates of mean frequency and the corresponding CVs were calculated. For bimanual trials, discrete estimates of the relative phase relation between the onset of EMG activity in the isometric and the dynamic limb were calculated for each homologous muscle pair (i.e. rFCR and lFCR; rECR and lECR), in the manner described above for the kinematic and kinetic recordings.

Inferential analyses

In order to restrict the analyses to those that have theoretical significance, the inferential statistics that are reported relate to the outcomes of planned comparisons of means, based on repeated measures analysis of variance (ANOVA) models. In performing these analyses, corrections for multiple comparisons (modified Bonferroni test) were conducted as appropriate (when the number of com-

[2] It should be noted that the thus obtained point estimates of relative phase are subject to small inaccuracies in cases in which the oscillatory pattern is not fully harmonic.

parisons exceeded the associated degrees of freedom), following Keppel (1991). In specific cases confidence intervals are also presented. In order to assist in the interpretation of the statistical significance of the observed effects, measures of effect size were calculated following Cohen (1969). The effect size index for ANOVA (*f*) is a dimensionless index which describes the degree of departure from no effect, in other words, the degree to which the phenomenon is manifested. A small effect size is considered by convention to be indicated by an *f* of 0.1, a medium effect size by an *f* of 0.25, and a large effect size by an *f* of 0.4 (Cohen 1969).

Results

Task performance

On the basis of the experimenters' observations and subjects' self-reports, it was evident that subjects experienced little difficulty in generating two distinct levels of torque, and in sustaining either level of torque throughout the duration of an experimental trial. As the two torque levels were not fully prescribed, the generated levels of torque were examined separately for each subject. Table 1 presents the mean values and 99% confidence intervals for each subject, for both the unimanual and bimanual conditions. It was also established that the two tempo requirements (1.0 Hz and 1.4 Hz) were adequately achieved (Table 2).

Table 3, which presents the mean direction of relative phase and the corresponding 99% confidence interval for each bimanual condition, shows that the subjects had adhered to the primary requirements of the bimanual task, that is, the production of the prescribed inphase (0°) and antiphase (180°) modes of coordination. There was a persistent tendency for the peak application of torque by the isometric hand to precede the peak displacement of the dynamic hand in time. This was not an unanticipated outcome, given the distinct dynamics associated with the two tasks. The magnitude of this effect, however, was not influenced in a marked fashion by the manipulations of force or frequency.

Timing and amplitude of joint displacements

Typical examples of the movement patterns of the dynamic hand, and the torque profiles of the isometric hand, as well as the corresponding EMG profiles are presented in Figs. 2 and 3. The characteristics of the motion of the dynamic hand were assessed in terms of the frequency and amplitude of movement, and the CVs of these variables. The actual frequency of movement was determined only by the prescribed frequency (cf. Table 2). In the bimanual conditions, the variability of timing was larger in the slow tempo conditions than in the fast conditions [mean CVs being 5.7% and 4.2%, respectively; $F(1, 5)=30.41$, $P<0.01$, $f=0.80$]. No such difference was observed when the standard deviation (SD) of frequency was used as the index of temporal variabili-

Table 1 Mean force level (in Nm) and corresponding 99% confidence interval presented for the two force conditions for each subject separately, both for unimanual and bimanual performance

	Comfort force		High force	
	Mean	Interval	Mean	Interval
Subject 1				
Unimanual	5.85	±1.78	11.49	±2.04
Bimanual	5.14	±0.56	11.82	±0.78
Subject 2				
Unimanual	2.41	±0.67	8.66	±0.90
Bimanual	4.90	±0.38	10.03	±0.64
Subject 3				
Unimanual	5.08	±1.40	12.39	±2.22
Bimanual	4.64	±0.74	11.15	±1.16
Subject 4				
Unimanual	2.61	±0.56	6.27	±0.68
Bimanual	2.55	±0.26	6.36	±0.35
Subject 5				
Unimanual	2.48	±0.45	6.79	±1.44
Bimanual	2.71	±0.33	6.74	±0.64
Subject 6				
Unimanual	3.72	±0.68	8.99	±1.11
Bimanual	3.79	±0.37	7.38	±0.40

Table 3 Mean direction of relative phase (in degrees) and the corresponding 99% confidence interval for the two bimanual coordination modes, as obtained for each tempo-force condition

Tempo	Force level	Inphase		Antiphase	
		Mean	Interval	Mean	Interval
1.0 Hz	Comfort	21.1	±9.5	–161.2	±17.0
	High	17.4	±11.4	–163.0	±14.2
1.4 Hz	Comfort	33.0	±11.1	–154.2	±23.6
	High	27.2	±12.7	–156.5	±23.7

Table 2 Mean frequency (in Hz) and corresponding 99% confidence interval for each tempo condition, presented for the two hands for both unimanual and bimanual performance

Hand	Condition	1.0 Hz		1.4 Hz		Preferred	
		Mean	Interval	Mean	Interval	Mean	Interval
Dynamic	Unimanual	1.01	±0.009	1.41	±0.008	1.08	±0.317
	Bimanual	1.01	±0.004	1.41	±0.003	–	–
Isometric	Unimanual	1.01	±0.004	1.41	±0.006	1.03	±0.276
	Bimanual	1.01	±0.003	1.41	±0.003	–	–

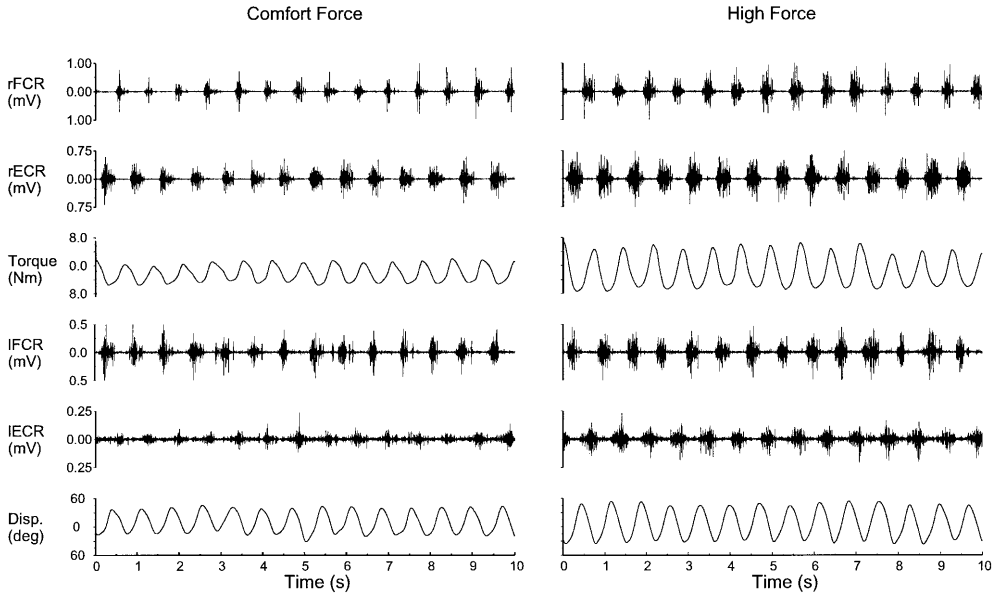

Fig. 2 Simultaneous EMG recordings from the right (*rFCR*) and left (*lFCR*) flexor carpi radialis muscles, and from the right (*rECR*) and left (*lECR*) extensor carpi radialis muscles. The corresponding kinematic and kinetic profiles are also presented. The panels on the *left* represent an antiphase trial conducted at a pacing frequency of 1.4 Hz, in which a comfort level of force was applied by the right (isometric) hand. The panels on the *right* represent an antiphase trial conducted at a pacing frequency of 1.4 Hz, in which a high level of force was applied by the right (isometric) hand. The data records, which were obtained for the same subject, are shown for a 10-s epoch. *EMG* electromyographic

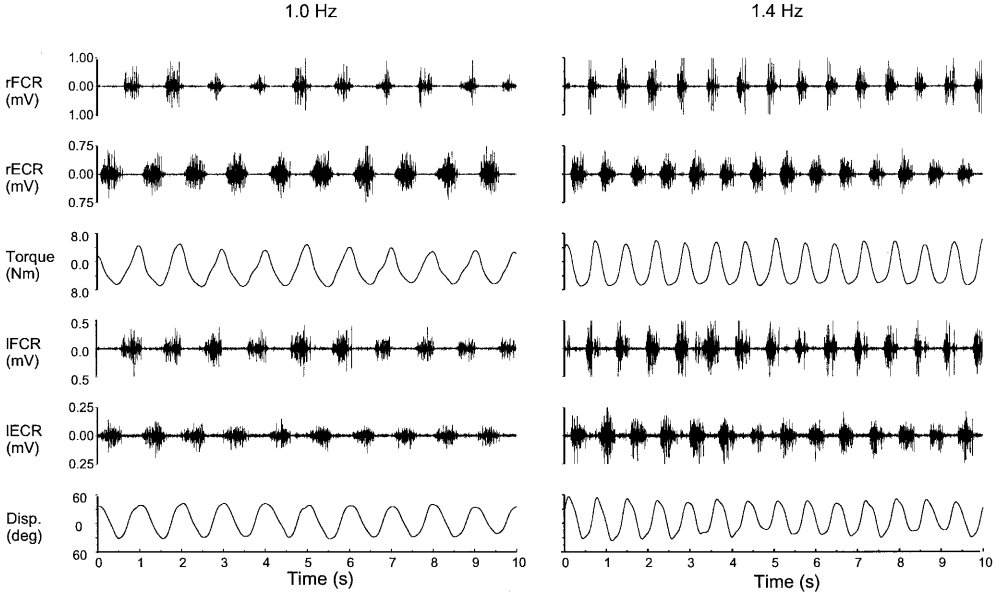

Fig. 3 Simultaneous EMG recordings from the right (*rFCR*) and left (*lFCR*) flexor carpi radialis muscles, and from the right (*rECR*) and left (*lECR*) extensor carpi radialis muscles. The corresponding kinematic and kinetic profiles are also presented. The panels on the *left* represent an inphase trial conducted at a pacing frequency of 1.0 Hz. The panels on the *right* represent an inphase trial conducted at a pacing frequency of 1.4 Hz. In both cases, a high level of force was applied by the right (isometric) hand. The data records, which were obtained for the same subject, are shown for a 10-s epoch. *EMG* electromyographic

ty. For the combination of slow tempo and high force, the CV of frequency was greater in both the inphase (6.3%) and the antiphase trials (6.2%) than in the corresponding unimanual trials [4.6%; $F(1, 45)=5.96$, $P<0.05$, $f=0.70$ and $F(1, 45)=5.75$, $P<0.05$, $f=0.69$, respectively]. Interestingly, the inphase and antiphase modes of coordination did not result in significant differences in this respect; $F(1, 5)=0.07$, $P>0.75$.

The amplitude of movement of the dynamic hand was influenced strongly by the context in which the hand was moving (see Fig. 4). In each of the eight bimanual conditions, the movement amplitude was smaller than when the hand was moving in isolation; $F(1, 45)$ ranging from 9.2 to 38.5, $P<0.05$ to 0.0001, $f=0.88$ to 1.79. In addition, the amplitudes of the movements were greater when the isometric hand was applying high levels of joint torque, than when comfort levels of torque were applied. The outcomes

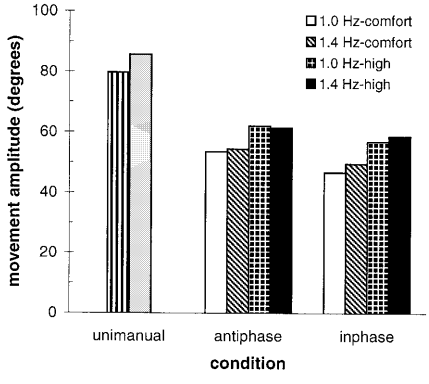

Fig. 4 Mean movement amplitudes generated by the dynamic hand for the two unimanual tempo conditions (1.0 Hz: *vertically striped bar*; 1.4 Hz: *grey bar*) and for each tempo-force condition as obtained for the two bimanual coordination modes

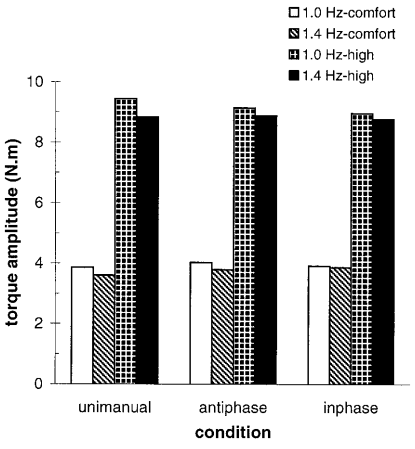

Fig. 5 Mean torque amplitudes of the isometric hand as obtained for each tempo-force condition, presented for unimanual performance and for the two bimanual coordination modes

of planned comparisons of means conducted for the two coordination modes and for the two frequency conditions, indicated that this effect was present in both the inphase and antiphase modes of bimanual coordination, as well as in the two tempo conditions [cf. Fig. 4; $F(1, 5)$ ranging from 23.9 to 64.7, $P<0.005$ to 0.0005, $f=1.00$ to 1.64]. Variability in the amplitude of oscillation, as indexed by the CV, was smaller during unimanual performance (overall mean of 6.0%) than in either bimanual coordination mode (overall means being 10.5% and 8.9% for inphase and antiphase coordination, respectively), as was determined by comparing the eight bimanual conditions with the corresponding unimanual conditions; $F(1, 45)$ ranging from 5.2 to 28.3, $P<0.05$ to 0.0001, $f=0.66$ to 1.54. In addition, the difference observed between the inphase and antiphase modes of coordination in this respect was statistically reliable; $F(1, 5)=8.3$, $P<0.05$, $f=0.42$.

Timing and amplitude of joint torques

The characteristics of the torque applied by the isometric hand were assessed in terms of the torque amplitude and frequency and the CVs of both variables. The frequency of torque application was determined only by the prescribed frequency (cf. Table 2). As anticipated, the target level of torque (i.e. comfort or high force) determined the actual level of applied torque (cf. Table 1). This variable was not influenced by the other experimental conditions: Torque amplitude was essentially equivalent in the unimanual and bimanual conditions, in the inphase and antiphase modes of bimanual coordination, and in the two tempo conditions (cf. Fig. 5).

In the unimanual conditions, the CV of torque amplitude was significantly larger for the comfort torque level than for the high torque level [on average 11.3% and 8.1%, respectively; $F(1, 5)=6.91$, $P<0.05$, $f=0.44$]. Furthermore, when paced at the slow tempo (1.0 Hz), the CV of torque amplitude was smaller in the unimanual trials (9.0%) than in either the inphase (11.1%) or antiphase (11.5%) modes of coordination; $F(1, 10)=6.4$, $P<0.038$[3], $f=0.52$ and $F(1, 10)=9.3$, $P<0.038$, $f=0.62$, also resulted

[3] On the basis of the modified Bonferroni test (Keppel 1991), the significance level was adjusted to 0.038 for the comparisons between unimanual and bimanual performance presented in this paragraph.

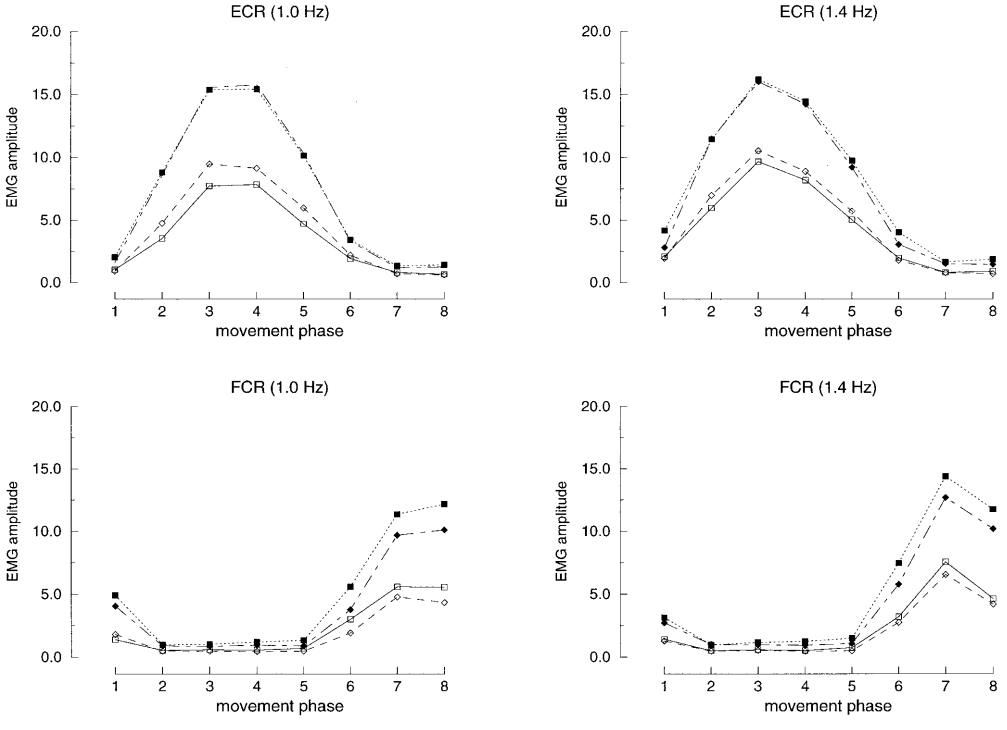

Fig. 6 Mean RMS amplitude of EMG recorded from the isometric limb in each phase of the movement cycle, presented for the flexor carpi radialis muscle (*FCR*) and extensor carpi radialis muscle (*ECR*). Phase 1 commences at peak torque in the direction of wrist flexion. The panels on the left correspond to movements paced at 1.0 Hz. The panels on the right correspond to movements paced at 1.4 Hz. *Open squares*: unimanual condition (comfort force); *filled squares*: unimanual condition (high force); *open diamonds*: bimanual condition (comfort force); *filled diamonds*: bimanual condition (high force). *RMS* root mean squared, *EMG* electromyogram

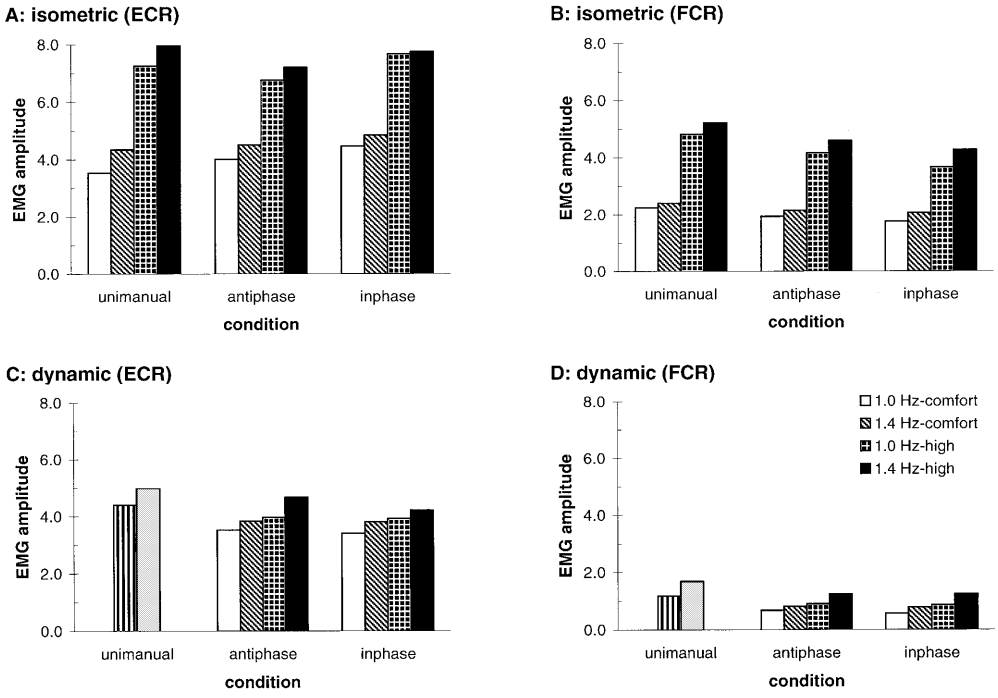

Fig. 7 Mean RMS amplitude of EMG recorded from the flexor carpi radialis muscle (*FCR*) and extensor carpi radialis muscle (*ECR*) of each limb, shown as a function of condition. In the unimanual conditions conducted for the dynamic limb (*panels C and D*), *vertically striped bars* refer to movements paced at 1.0 Hz, and *grey bars* correspond to movements paced at 1.4 Hz. *RMS* root mean squared, *EMG* electromyogram

in smaller values of respectively. The slow tempo conditions also resulted in smaller values of the CV of the frequency of torque application in the unimanual conditions (4.6%) than in the inphase mode of coordination (5.5%); $F(1, 10)=6.8$, $P<0.038$, $f=0.54$. During bimanual coordination, the temporal variability of performance was greater in the slow conditions than in the fast conditions (5.4% and 4.3%, respectively); $F(1, 5)=7.5$, $P<0.05$, $f=0.40$. Note that these conditions did not differ with regard to the SD of frequency.

Amplitude of electromyographic activity

Fig. 6 portrays the RMS amplitude of EMG activity recorded from the ECR and FCR muscles of the isometric limb during the eight phases of the movement cycle. Activity in both muscles was modulated markedly during the movement cycle. The ECR muscle was engaged primarily during phases 2, 3, 4, and 5. FCR was engaged in a reciprocal fashion, primarily during phases 6, 7, and 8. In accordance with our expectations, the amplitude of EMG recorded during the active phases of both muscles of the isometric limb was substantially greater when high levels of force were applied than when comfort levels of force were produced [see also Fig. 7, panels A and B; ECR: $F(1, 5)=21.32$, $P<0.01$, $f=0.19$; FCR: $F(1, 5)=12.02$, $P<0.01$, $f=0.14$]. In contrast, the frequency with which force was to be applied did not have a significant influence on the level of EMG activity recorded from the muscles of the isometric limb. The mode of coordination (unimanual, antiphase, inphase) had no consistent impact on the level of EMG activity (cf. Fig. 7).

Table 4 Results of planned comparisons of means, testing the effect of force level (comfort vs high force), as applied by the isometric hand, for each tempo-mode condition for both the extensor carpi radialis muscle (*ECR*) and the flexor carpi radialis muscle (*FCR*) of the dynamic limb. Significant comparisons are indicated by *

Muscle	Tempo	Mode	$F(1, 45)$	P	f
ECR	1.0 Hz	Antiphase	5.15	<0.05*	0.23
ECR	1.0 Hz	Inphase	6.86	<0.05*	0.27
ECR	1.4 Hz	Antiphase	18.41	<0.01*	0.44
ECR	1.4 Hz	Inphase	4.21	<0.05*	0.21
FCR	1.0 Hz	Antiphase	1.37	>0.20	0.12
FCR	1.0 Hz	Inphase	2.38	>0.10	0.16
FCR	1.4 Hz	Antiphase	4.47	<0.05*	0.22
FCR	1.4 Hz	Inphase	5.63	<0.05*	0.24

The EMG activity obtained from the dynamic limb showed a similar modulation over the movement cycle (see Fig. 8). The amplitude of the EMG activity recorded from the muscles of this limb, however, was influenced significantly by the activity of the other limb (see Fig. 7, panels C and D). There was greater muscle activation when the hand was moving in isolation than when its movements were coordinated with applications of force by the isometric hand [ECR: $F(1, 45)=50.20$, $P<0.01$, $f=0.40$; FCR: $F(1, 45)=25.12$, $P<0.01$, $f=0.29$]. In addition, the outcomes of planned comparisons of means indicated that, in both the inphase and antiphase modes of bimanual coordination, the level of force applied by the isometric hand had a marked and consistent impact on the level of EMG activity recorded from the muscles of the dynamic limb (see Table 4). When a higher level of force was applied by the isometric limb, greater levels of EMG activity were obtained for the dy-

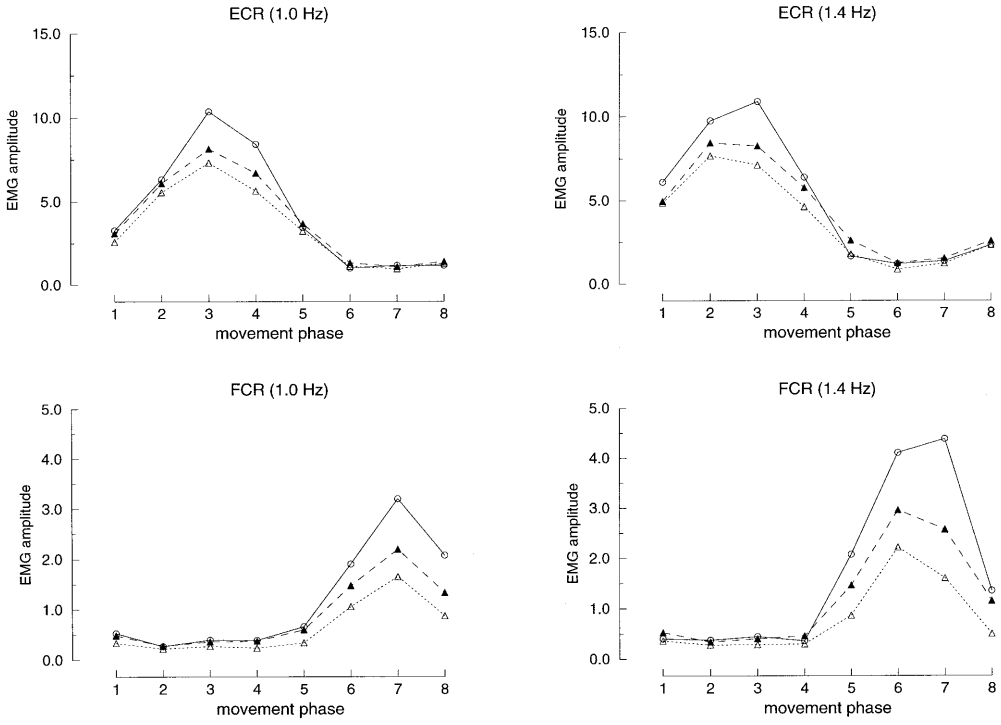

Fig. 8 Mean RMS amplitude of EMG recorded from the dynamic limb in each phase of the movement cycle, presented for the flexor carpi radialis muscle (*FCR*) and extensor carpi radialis muscle (*ECR*). Phase 1 commences at peak flexion of the wrist. The panels on the left correspond to movements paced at 1.0 Hz. The panels on the right correspond to movements paced at 1.4 Hz. *Open circles*: unimanual condition; *open triangles*: bimanual condition (comfort force); *filled triangles*: bimanual condition (high force). *RMS* root mean squared, *EMG* electromyogram

namic limb than in the comfort force conditions (cf. Fig. 7). On initial inspection, it appeared that this effect was expressed reliably for the ECR muscle at both pacing frequencies, whereas for the FCR muscle it occurred only when performance was paced at a frequency of 1.4 Hz (cf. Table 4). When the analyses were restricted to the phases of the movement during which the FCR muscle was primarily active (phases 6, 7, and 8), however, reliable differences between the comfort and high force conditions were also obtained for inphase coordination paced at 1.0 Hz; $F(1, 315)=3.94$, $P<0.05$, $f=0.33$. In contrast, the pattern of bimanual coordination (inphase vs antiphase) in which the movements were prepared had no significant impact on the level of EMG activity recorded from either the ECR muscle or the FCR muscle of the dynamic limb. The level of EMG activity recorded from this limb was larger for performance at 1.4 Hz than that obtained when the hand oscillated at 1.0 Hz [ECR: $F(1, 45)=27.51$, $P<0.01$, $f=0.24$; FCR: $F(1, 45)=12.96$, $P<0.01$, $f=0.16$].

Variability in the timing of electromyographic activity

For the unimanual performance of either limb, no statistically significant effects of tempo or force level on the variability of the timing of EMG burst onsets were obtained. During bimanual performance, however, the dynamic limb showed larger variability in the timing of EMG onsets in the slow tempo condition than in the fast condition [see Table 5; $F(1, 5)=20.1$, $P<0.01$, $f=0.46$]. The timing of the activation of the ECR muscle of this limb was less variable in the unimanual conditions

Table 5 CV of frequency as obtained for the electromyographic activity (collapsed over extensor carpi radialis (ECR) and flexor carpi radialis (FCR)) of the two limbs during bimanual performance, presented for the two coordination modes, the two force conditions, and the two tempo conditions

	Dynamic	Isometric
Coordination mode		
Inphase	18.50	6.20
Antiphase	14.33	6.17
Force Level		
Comfort	17.01	6.98
High	15.83	5.40
Frequency		
1.0 Hz	21.31	7.31
1.4 Hz	11.53	5.07

(8.9%) than in inphase coordination at the slow tempo condition, both when comfort [19.2%; $F(1, 45)=4.3$, $P<0.05$, $f=0.60$], and high [21.3%; $F(1, 45)=6.2$, $P<0.05$, $f=0.72$] levels of torque were applied. No such effects were observed for the FCR muscle. In the high torque conditions, the variability in the timing of the EMG onsets of the ECR muscle of the isometric limb was higher during unimanual performance than during inphase coordination [7.7% and 4.8%, respectively; $F(1, 10)=5.74$, $P<0.038$, $f=0.49$]. In the bimanual conditions, the timing of the EMG onsets of the muscles of the dynamic limb was significantly more variable than that of the muscles of the isometric limb, in both modes of coordination, at both levels of torque, and for the slow tempo

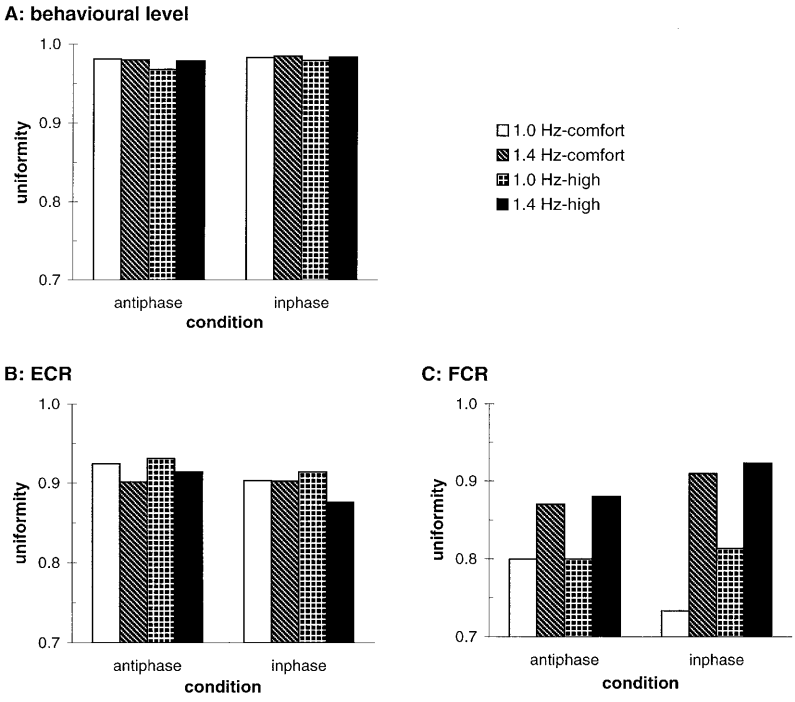

Fig. 9 Uniformity of relative phase as obtained at the behavioural level (*panel A*) and at the level of the electromyographic activity recorded from the extensor carpi radialis muscle (*ECR: panel B*) and flexor carpi radialis muscle (*FCR: panel C*), presented separately for each tempo-force condition in the two bimanual coordination modes

condition [see Table 5; $F(1, 5)$ ranging from 15.5 to 213.4, $P<0.025$ to 0.0001, $f=0.40$ to 1.49].

Interlimb coordination

The effects of the experimental manipulations on the variability of relative phase, an index of pattern stability, were examined both at the behavioural level and at the neuromuscular level (see Fig. 9). At the behavioural level, no statistically significant effects were observed. Reliable differences were also not expressed in the coordination of the ECR muscles. For the FCR muscles, however, the uniformity of relative phase was lower (indicating greater variability) during performance in the slow tempo condition than in the fast condition [see Fig. 9C; $F(1, 5)=19.6$, $P<0.01$, $f=0.64$]. The inphase and antiphase modes of coordination were not distinguished in terms of their stability, when assessed at either the behavioural or the neuromuscular levels of observation.

Discussion

The current experiment was designed to examine the influence of rhythmic voluntary activation of the muscles of one limb on the movement patterns of the contralateral limb. Contractions of the muscles of the former (isometric) limb were performed with the hand in a fixed position. It was reasoned that this manipulation would alter the integration of somatosensory feedback from this limb relative to circumstances in which movement amplitude was unconstrained. Inspired by previous studies and a dynamical model of isochronous rhythmic interlimb coordination (the HKB model), the effects of tempo, coordination mode, and different levels of voluntary activation on the stability of coordination between the two limbs were also examined. The results are discussed in the light of previous studies, and with regard to the neurophysiological mechanisms that may underpin the stability of bimanual coordination.

The effects of different levels of voluntary activation on contralateral movement amplitude

In correspondence with the task instructions, the level of torque applied by the isometric hand was equivalent in the unimanual and bimanual conditions. The amplitude of movement of the dynamic hand, however, was reduced markedly in the coupled (bimanual) conditions, relative to circumstances in which the hand moved in isolation. In addition, it was significantly affected by the level of torque applied by the contralateral hand. When subjects applied a high level of torque with the isometric hand, the associated movements of the freely moving hand were of a larger amplitude than when a lower (comfort) level of torque was applied. These observations are consistent with those reported by Walter and Swinnen (1990) for a bimanual task that required the coordination of a three-segment reversal movement of the right arm, with a smooth unidirectional movement of the left arm. Manipulation of the level of torque necessary to produce the reversal movement, resulted in systematic alterations in the acceleration profile of the unidirectional movement produced by the contralateral arm. In contrast, manipulation of the duration of the reversal movement, independently of the required torque, failed to

have an impact on the kinematic trajectory of the contralateral limb. Similarly, in the present study, the frequency with which torque was applied by the isometric limb did not influence the effect of the level of torque on the amplitude of the movements of the dynamic limb.

Directly corresponding outcomes were obtained at the neuromuscular level of observation. The amplitude of EMG activity recorded during unimanual movements of the dynamic limb was greater than that present during movements made in a bimanual context. Furthermore, when subjects were required to produce a high level of torque with the isometric hand, there was greater EMG activity than in the comfort condition, not only in the muscles of the isometric limb, but also in the muscles of the unconstrained (dynamic) contralateral limb. These results suggest that the variations in movement amplitude observed for the unconstrained limb resulted from changes in the net excitability of the motoneurone pools, rather than from, for example, alterations in the degree of co-contraction of the muscles that flex and extend the wrist.

The effects of different levels of voluntary activation on movement variability

In the present study, the level of torque generated by the isometric hand had a restricted impact on the variability of movement of the unconstrained contralateral limb, as assessed at both the behavioural and neuromuscular levels of observation. Although the variability of the amplitude of oscillation was smaller during single limb movements than during bimanual movements, in the latter conditions there was no additional effect attributable to the level of applied torque. At the lower pacing frequency, the temporal variability of the dynamic hand was greater when high levels of torque were applied by the isometric hand than during the unimanual control trials. This effect did not simply reflect the variability in the frequency with which torque was applied by the contralateral (isometric) limb, which was equivalent in both force conditions. The fact that the generated force level affected the temporal variability in both hands supports the suggestion that in case the control of force amplitude and timing involves relatively independent processes, possibly involving different neural systems (Franz et al. 1996; Ivry and Corcos 1993; Lundy-Ekman et al. 1991), they are integrated during the production of movement (Keele et al. 1987).

Whereas the level of applied force affected the temporal variability of the dynamic limb, the variability of the temporal relation between the limbs (relative phase) for either of the two bimanual coordination patterns (inphase and antiphase) was not influenced significantly. This indicated that although the level of voluntary activation had clear effects on the movements of the contralateral hand (viz. the effects obtained for the amplitudes of oscillation of the moving hand as well as that observed for its temporal variability), these effects did not influence the stability of interlimb coordination.

The influence of tempo and mode on the stability of coordination

During performance at the slower tempo, in combination with the higher force level, the variability of timing was larger during bimanual movements than during the unimanual control trials.[4] There was no effect of tempo, however, on the stability of interlimb coordination (as indexed by the uniformity of relative phase), when assessed at the behavioural level. This is a remarkable finding, as it indicates that, at this level of analysis, no differences in pattern stability were induced by the manipulation of movement tempo. Although the results of previous experiments, in which frequency of performance was gradually scaled, suggest that variability of relative phase is different for the two pacing frequencies used in the present study (e.g. Carson 1995; Jeka and Kelso 1995; Peper and Beek 1998b), it is possible that in the current context the change in frequency (0.4 Hz) was too small to lead to significant differences in pattern stability. Although, at present, we cannot exclude this possibility, it should be noted that at the neuromuscular level (FCR) the stability of interlimb coordination was lower in the slow tempo conditions than in the fast conditions. This indicates that pattern stability was positively related to movement frequency, a finding that is directly opposite to the relation predicted by the HKB model.

The values of uniformity obtained at the behavioural level were high (cf. Fig. 9A) indicating rather stable performance of both coordination patterns (cf. Carson 1995; Peper and Beek 1998b). At the neuromuscular level the corresponding values were somewhat lower (cf. Fig. 9B, C). As the variability in the timing of the EMG onsets in individual muscles was larger in the slow tempo conditions than in the fast conditions, it is possible that the changes in the variability of interlimb coordination that occurred as a function of tempo were attributable to speed-sensitive variations in the activation profiles of individual EMG bursts (e.g. Gottlieb et al. 1989).

No overall differences in pattern stability between the two coordination modes were observed. This finding is in sharp contrast with many previous studies, in which (in a manner consistent with the HKB model) the antiphase pattern has been observed to be less stable than the inphase pattern, even at relatively low pacing frequencies equivalent to those employed in the present experiment (e.g. Amazeen et al. 1995; Amazeen et al. 1996; Sternad et al. 1996; see also Kelso et al. 1987). The absence of differences in stability between the two coordination modes and between the two tempo conditions indicates that the present results are not in agreement with the HKB model of rhythmic interlimb coordination. Although some caution is required in interpreting the lack of difference between the tempo conditions, as only a limited range of frequencies were examined, our inter-

[4] Note that because the comparisons of unimanual and bimanual coordination concerned performance at the same tempo, differences in performance between the two conditions could not have arisen from variations in mean frequency.

pretation of the results obtained for the two coordination modes carries no such caveat. The deviations from the commonly observed stability characteristics that were found in the current context may provide some indications of the neurophysiological origins of stability and instability in rhythmic interlimb coordination.

Possible neurophysiological aspects of modulations of pattern stability

In the present study there was significant interaction between the limbs, as indicated by the influence of the activity of the isometric limb upon the muscle activation profile and the movement pattern of the dynamic limb. Yet the two modes of bimanual coordination (inphase and antiphase) were not distinguished in terms of their stability, and an inverse relationship between movement frequency and pattern stability was not observed. These findings indicate that the stability characteristics of rhythmic bimanual coordination are contingent on the task context. Interestingly, the present results were clearly different from those obtained for the coordination between two actively moving limbs (e.g. Haken et al. 1985) as well as from those obtained when both limbs were engaged in isometric applications of torque (Carson 1995). It appears, therefore, that the absence of the prototypical stability characteristics in the present study was due to the imposed asymmetry with respect to the task requirements.

In modelling rhythmic interlimb coordination, such differences in the stability characteristics resulting from specific influences associated with the task performance will have to be considered. For instance, the coordination dynamics that typically results from the interactions between two actively moving limbs was recently accounted for by a central pattern generator model proposed by Grossberg et al. (1997). In this model the stability-related phenomena (i.e. differential stability and frequency-induced transitions) were understood on the basis of a pattern generator that was shown to produce a temporal activation pattern similar to the empirically observed time evolution of the phase relation between the limbs. The current results indicate that this model cannot be directly generalised to situations in which the tasks assigned to the two limbs are not equivalent. To this end, the influences of particular task-specific aspects of the coordination will have to be incorporated. This might entail, for instance, motivated adjustments in parameter settings, or the inclusion of additional model components and interactions. With respect to the HKB model it may be argued that, instead of accounting for the current results at the level of the potential function, considering the specific consequences for the associated system of coupled oscillators is more likely to lead to new insights into the underlying coordination principles. Studying the way in which distinct neurophysiological mechanisms affect the stability of coordination may provide vital information for establishing which aspects of task performance are essential in this regard.

A number of neurophysiological mechanisms may account for the differences between the behavioural dynamics observed in the current study, and those present when both limbs are free to move or when both are performing rhythmic isometric contractions. These mechanisms are not mutually exclusive, and may even be interdependent. One possibility is that, in isometric contractions and dynamic movements, different roles may be afforded to mechanisms that regulate the gain of transmission of segmental inputs to the motoneurone pool. Another possible explanation may be found in asymmetries in the recruitment of motor units. In the remainder of this section these possibilities will be discussed. In each case, consideration will be given to the manner in which the operation of such mechanisms may constrain the nature of the interaction between the limbs.

As has been argued in the Introduction, it is now clear that the movement of a single limb segment may lead to modification of the excitability of the contralateral Ia spinal reflex pathway (Carson et al. 1999; McIlroy et al. 1992). The extent of this contralateral influence increases with the velocity of movement (Collins et al. 1993). It has been proposed that entrainment tendencies mediated by peripheral input arising from movement, may provide a means by which limbs that are initially moving out of phase become synchronised (Carson and Riek 1998; Hasan et al. 1985). During voluntary movements, the spinal circuitry is responsible for the integration of descending and peripheral inputs. The impaired performance customarily associated with less stable modes of coordination (e.g. antiphase coordination) may arise because the motor commands from higher centres are not able to compensate sufficiently for entrainment in spinal motor circuits that results from movement-elicited afference from the contralateral limb (e.g. Baldissera et al. 1991; Carson et al. 1999).

During voluntary contractions there is parallel and orderly recruitment of both skeletomotor neurones and fusiomotor neurones (e.g. Burke et al. 1978). Such α-γ coactivation assumes a highly functional role during shortening contractions, by providing spindle endings with a background discharge sufficient to permit compensation for irregularities in the ongoing movement. During isometric contractions, however, the descending drive to fusiomotor neurones, which is not accompanied by unloading of the spindle and results in augmented spindle afferent discharge, can be maladaptive. In these circumstances presynaptic inhibition of the Ia afferents may serve to prevent motoneurones from being reflexly activated by spindle discharge (Schieppati 1992). Evidence in support of this position is provided by the observation of a parallel reduction in the size of motor-evoked potentials and H-reflexes during isometric contractions, relative to those elicited during shortening contractions (Abbruzzese et al. 1994). These data suggest the presence of spinal mechanisms that modulate the gain of transmission to the motoneurone pool (via both afferent and descending pathways) differentially during isometric and shortening contractions (Abbruzzese et al. 1994). It

also appears likely, therefore, that the gain of transmission of peripheral input from the contralateral limb, when it is moving dynamically, will be distinct from that which occurs when the opposite limb is engaged in isometric contractions. Accordingly, the current results may suggest that the normally defining stability characteristics of bimanual coordination are contingent upon a correspondence between the limbs, in terms of the manner in which sensory feedback is integrated to produce task-specific muscle-activation patterns.

It is not necessary to conclude, however, that differences between dynamic movements and isometric contractions, in terms of the integration of afferent input, are mediated only by the spinal circuitry. Indeed, on the basis of recordings of regional cerebral blood flow during active and passive movements, it appears that the activation of the higher centres during motor tasks is largely related to the processing of afferent information arising from movement (Weiller et al. 1996). Comparison of stretch reflex responses elicited during tasks in which subjects are required to maintain position against a changing force with those elicited during tasks in which subjects are required to maintain force against a changing position, demonstrated that in particular the late components of the reflex were greater in the former situation (Doemges and Rack 1992a; Doemges and Rack 1992b). In circumstances in which a constant level of EMG was maintained across tasks, the late components of the stretch reflex were found to be larger during shortening contractions than during isometric contractions (Nakazawa et al. 1997). It has been proposed that such task dependencies arise from differences in the gating of afferent information (Dietz et al. 1994; cf. Schieppati 1992). In a similar vein, it seems likely that muscle spindle discharge is the initiating source for the modulation of somatosensory-evoked potentials that arises as a consequence of movement of both the ipsilateral and the contralateral limb (Staines et al. 1998). The gain of transmission of this information, via ascending pathways, is influenced profoundly by the task context (Staines et al. 1997). If the specific pathways to and from the higher centres, that are gated during isometric contractions, are distinct from those that are regulated during dynamic movements, there may be relatively little potential for contralateral influences upon homologous pathways to be expressed in the combination of these tasks.

It is also possible that the absence of a difference in stability between the coordination patterns was contingent upon task-related variations in the recruitment of motor units. It is well known that the recruitment levels and firing frequencies of motor units are different in isometric and in shortening contractions (Tax et al. 1989; Tax et al. 1990). Such differences are also observed when individuals are required to produce either sinusoidal isometric contractions or sinusoidal movements (Van Bolhuis et al. 1997). Can such organisational form be related to the current results? There are linkages between homotopic sites at multiple levels within the central nervous system, that mediate contralateral influences upon motor pathways. It is clear that, during bimanual coordination, the coupling between the limbs is accentuated when homologous muscles are co-activated (Riek et al. 1992). The current results may tentatively suggest that the degree of interaction between the limbs is enhanced when the subpopulations of motor units in each limb that are recruited in order to perform a specific task (e.g. an isometric contraction vs a dynamic movement) are equivalent.

In summary, the present results suggest that the interactions between the limbs, during bimanual coordination, are influenced profoundly by the task context. In particular, defining characteristics of rhythmic bimanual coordination, such as the differential stability of inphase and antiphase modes, and an inverse relationship between movement frequency and pattern stability, appear to be contingent upon a correspondence between the limbs in terms of task. Our interpretation of these results highlighted both the possible role of sensory information from the moving limb in ‘normal’ (i.e. functionally symmetric) interlimb coordination, and the functional specificity of motor unit recruitment patterns. On the basis of the present results we cannot establish the relative contributions of the proposed neurophysiological mechanisms to the coordination dynamics. In fact, follow-up research is required to determine whether they are indeed essential in this regard. Nevertheless, the present study illustrates how the abstract coordination dynamics (which directs our attention to the stability and instability of coordination patterns) may provide an entry point for the identification of the neural systems that are involved in the coordination between the limbs during rhythmic movements. At the same time, the present findings accentuate the importance of ‘unpacking’ the HKB potential into a system of coupled oscillators, which corresponds in a more direct manner to established characteristics of the neuromuscular system (cf. Peper and Beek 1998b; Peper and Beek 1999).

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References

Abbruzzese G, Morena M, Spadavecchia L, Schieppati M (1994) Response of arm flexor muscles to magnetic and electrical brain stimulation during shortening and lengthening tasks in man. J Physiol (Lond) 481: 490–507

Aizawa H, Mushiake H, Inase M, Tanji J (1990) An output zone of the monkey primary motor cortex specialized for bilateral hand movements. Exp Brain Res 82: 219–221

Amazeen PG, Schmidt RC, Turvey MT (1995) Frequency detuning of the phase entrainment dynamics of visually coupled rhythmic movements. Biol Cybern 72: 511–518

Amazeen EL, Sternad D, Turvey MT (1996) Predicting the nonlinear shift of stable equilibria in interlimb rhythmic coordination. Hum Mov Sci 13: 521–542

Baldissera F, Cavallari P, Civaschi P (1982) Preferential coupling between voluntary movements of ipsilateral limbs. Neurosci Lett 34: 95–100

Baldissera F, Cavallari P, Marini G, Tassone G (1991) Differential control of in-phase and anti-phase coupling of rhythmic movements of ipsilateral hand and foot. Exp Brain Res 83: 375–380

Baldissera F, Cavallari P, Leocani L (1998) Cyclic modulation of the H-reflex in a wrist flexor during rhythmic flexion-extension movements of the ipsilateral foot. Exp Brain Res 118: 427–430

Brinkman C, Porter R (1979) Supplementary motor area in the monkey: activity of neurons during performance of a learned motor task. J Neurophysiol 42: 681–709

Brooke JD, McIlroy WE, Collins DF (1992) Movement features and H-reflex modulation. I. Pedalling versus matched controls. Brain Res 582: 78–84

Brooke JD, Cheng J, Misiaszek JE, Lafferty K (1995) Amplitude modulation of the soleus H reflex in the human during active and passive stepping movements. J Neurophysiol 73: 102–111

Brooke JD, Cheng J, Collins DF, McIlroy WE, Misiaszek JE, Staines WR (1997) Sensori-sensory afferent conditioning with leg movement: gain control in spinal reflex and ascending paths. Prog Neurobiol 51: 393–421

Brown DA, Kukulka CG (1993) Human flexor reflex modulation during cycling. J Neurophysiol 69: 1212–1224

Burke D, Hagbarth K-E, Löfstedt L (1978) Muscle spindle activity in man during shortening and lengthening contractions. J Physiol (Lond) 277: 131–142

Burke D, Gandevia SC, McKeon B (1984) Monosynaptic and oligosynaptic contribution to human ankle jerk and H-reflex. J Neurophysiol 52: 434–448

Buys EJ, Lemon RN, Mantel GWH, Muir RB (1986) Selective facilitation of different hand muscles by single corticospinal neurones in the conscious monkey. J Physiol (Lond) 381: 529–549

Byblow WD, Chua R, Goodman D (1995) Asymmetries in coupling dynamics of perception and action. J Mot Behav 27: 123–137

Capaday C, Stein RB (1986) Amplitude modulation of the soleus H-reflex in the human during walking and standing. J Neurosci 6: 1308–1313

Capaday C, Stein RB (1987) Difference in the amplitude of the human soleus H reflex during walking and running. J Physiol 392: 513–522

Carson RG (1995) The dynamics of isometric bimanual coordination. Exp Brain Res 105: 465–476

Carson RG, Riek S (1998) Moving beyond phenomenology: neuromuscular-skeletal constraints on coordination dynamics. In: Piek JP (ed) Motor control and human skill: a multidisciplinary perspective. Human Kinetics, Champaign IL, pp 209–230

Carson RG, Goodman D, Kelso JAS, Elliott D (1995) Phase transitions and critical fluctuations in rhythmic coordination of ipsilateral hand and foot. J Mot Behav 27: 211–224

Carson RG, Riek S, Bawa P (1999) Electromyographic activity, H-reflex modulation, and corticospinal input to forearm motoneurones during active and passive rhythmic movements. Hum Mov Sci 18:307–343

Cheney PD, Fetz EE (1985) Comparable patterns of muscle facilitation evoked by individual corticomotoneuronal (CM) cells and by single intracortical microstimuli in primates: evidence for functional groups. J Neurophysiol 53: 786–804

Cheng J, Brooke JD, Misiaszek JE, Staines WR (1995) The relationship between the kinematics of passive movement, the stretch of extensor muscles of the leg and the change induced in the gain of the soleus H reflex in humans. Brain Res 672: 89–96

Cheng J, Brooke JD, Misiaszek JE, Staines WR (1998) Crossed inhibition of the soleus H reflex during passive pedalling movement. Brain Res 779: 280–284

Chiappa KH, Cros D, Day B, Fabg J, MacDonell R, Mavroudakis N (1991) Magnetic stimulation of the human motor cortex: ipsilateral and contralateral facilitation effects. In: Levy WJ, Cracco RQ, Barker AT, Rothwell J (eds) Magnetic motor stimulation: basic principles and clinical experience (Electroencephalogr Clin Neurophysiol Suppl 43). Elsevier, Amsterdam, pp 186–201

Cohen J (1969) Statistical power analysis for the behavioral sciences. Academic Press, New York

Cohen L (1970) Interaction between limbs during bimanual voluntary activity. Brain 93: 259–272

Cohen L (1971) Synchronous bimanual movements performed by homologous and non-homologous muscles. Percept Mot Skills 32: 639–644

Collins DF, McIlroy WE, Brooke JD (1993) Contralateral inhibition of soleus H reflexes with different velocities of passive movement of the opposite leg. Brain Res 603: 96–101

Crenna P, Frigo C (1987) Excitability of the soleus H-reflex arc during walking and stepping in man. Exp Brain Res 66: 49–60

Dietz V, Discher M, Trippel M (1994) Task-dependent modulation of short- and long-latency electromyographic responses in upper limb muscles. Electroencephalogr Clin Neurophysiol 93: 49–56

deGuzman CG, Kelso JAS (1991) Multifrequency behavioral patterns and the phase attractive circle map. Biol Cybern 64: 485–495

Doemges F, Rack PMH (1992a) Changes in stretch reflex of the human first dorsal interosseous muscle during different tasks. J Physiol (Lond) 447: 563–573

Doemges F, Rack PMH (1992b) Task-dependent changes in the response of human wrist joints to mechanical disturbance. J Physiol (Lond) 447: 575–585

Farmer SF, Ingram DA, Roche SW, Stephens JA (1989) Evidence that mirror movements in the Klippel-Feil syndrome in man are produced by activity in branched-stem presynaptic inputs from corticospinal neurons. J Physiol (Lond) 418: 102P

Franz EA, Ramachandran VS (1998) Bimanual coupling in amputees with phantom limbs. Nature Neurosci 1: 443–444

Franz EA, Eliassen JC, Ivry RB, Gazzaniga MS (1996) Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. Psychol Sci 7: 306–310

Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G (1988) Functional organization of inferior area 6 in the macaque monkey. Exp Brain Res 71: 475–490

Gottlieb GL, Corcos DM, Agarwal GC (1989) Strategies for the control of voluntary movements with one mechanical degree of freedom. Behav Brain Sci 12: 189–250

Grossberg S, Probe C, Cohen MA (1997) Neural control of interlimb oscillations: I. Human bimanual coordination. Biol Cybern 77: 131–140

Gunkel M (1962) Relative coordination in voluntary limb movements in man (in German). Pflügers Arch 275: 427–477

Haken H, Kelso JAS, Bunz H (1985) A theoretical model of phase transitions in human hand movements. Biol Cybern 51: 347–356

Hasan Z, Enoka RM, Stuart DG (1985) The interface between biomechanics and neurophysiology in the study of movement: some recent approaches. Exerc Sport Sci Rev 13: 169–234

Hess CW, Mills KR, Murray NMF (1986) Responses in small hand muscles from magnetic stimulation of the human brain. J Physiol 388: 397–419

Hess CW, Mills KR, Murray NMF (1987) Magnetic stimulation of the human brain: facilitation of motor responses by voluntary contraction of ipsilateral and contralateral muscles with additional observations in an amputee. Neurosci Lett 71: 235–240

Ivry RB, Corcos DM (1993) Slicing the variability pie: component analysis of coordination and motor dysfunction. In: Newell KM, Corcos DM (eds) Variability and motor control. Human Kinetics, Champaign, Ill., pp 415–447

Jeka JJ, Kelso JAS (1995) Manipulating symmetry in the coordination dynamics of human movement. J Exp Psychol Hum Percept Perform 21: 360–374

Keele SW, Ivry RB, Pokorny RA (1987) Force control and its relation to timing. J Mot Behav 19: 96–114
Kelso JAS (1984) Phase transitions and critical behavior in human bimanual coordination. Am J Physiol: Reg, Integr Comp Physiol 15: R1000-R1004
Kelso JAS, Southard DL, Goodman D (1979) On the coordination of two-handed movements. J Exp Psychol: Hum Percept Perform 2: 229–238
Kelso JAS, Schöner G, Scholz JP, Haken H (1987) Phase-locked modes, phase transitions and component oscillators in biological motion. Phys Scr 34: 79–87
Kelso JAS, DelColle JD, Schöner G (1990) Action-perception as a pattern formation process. In: Jeannerod M (ed) Attention and performance XII. Lawrence Erlbaum, Hillsdale, N.J., pp 139–169
Keppel G (1991) Design and analysis: a researcher's handbook (third edn). Prentice-Hall, Englewood Cliffs, NJ
Lundy-Ekman L, Ivry RB, Keele SW, Woollacott M (1991) Timing and force control deficits in clumsy children. J Cogn Neur 3: 367–376
Mardia KV (1972) Statistics of directional data. Academic Press, London
Marteniuk RG, MacKenzie CL, Baba DM (1984) Bimanual movement control: information processing and interaction effects. Q J Exp Psychol 36A: 335–356
Matsunami K, Hamada I (1981) Characteristics of the ipsilateral movement-related neuron in the motor cortex of the monkey. Brain Res 204: 29–42
McIlroy WE, Collins DF, Brooks JD (1992) Movement features and H-reflex modulation. II. Passive rotation, movement velocity and single leg movements. Brain Res 582: 85–93
Nakazawa K, Yamamoto S, Yano H (1997) Short- and long-latency reflex responses during different motor tasks in elbow flexor muscles. Exp Brain Res 116: 20–28
Peper CE, Beek PJ (1998a) Distinguishing between the effects of frequency and amplitude on interlimb coupling in tapping a 2:3 polyrhythm. Exp Brain Res 118: 78–92
Peper CE, Beek PJ (1998b) Are frequency-induced transitions in rhythmic coordination mediated by a drop in amplitude? Biol Cybern 79: 291–300
Peper CE, Beek PJ (1999) Modeling rhythmic interlimb coordination: the roles of movement amplitude and time delays. Hum Mov Sci 18:263–280
Riek S, Carson RG, Byblow WD (1992) Spatial and muscular dependencies in bimanual coordination. J Hum Mov Stud 23: 251–265
Romanò C, Schieppati M (1987) Reflex excitability of human soleus motoneurones during voluntary shortening or lengthening contractions. J Physiol 390: 271–284
Rothwell JC (1994) Control of human voluntary movement. Chapman and Hall, London
Schieppati M (1992) Selection of task-related motor output through spinal motoneurones. Behav Brain Sci 15: 794–795
Schmidt RC, Carello C, Turvey MT (1990) Phase transitions and critical fluctuations in the visual coordination of rhythmic movement between people. J Exp Psychol Hum Percept Perform 16: 227–247
Staines WR, Brooke JD, Cheng J, Misiaszek JE, MacKay WA (1997) Movement-induced gain modulation of somatosensory potentials and soleus H-reflexes evoked from the leg. Exp Brain Res 115: 147–155
Staines WR, Brooke JD, Angerilli PA, McIlroy WE (1998) Generalisability of sensory gating during passive movement of the legs. Brain Res 801: 125–129
Stein RB (1995) Presynaptic inhibition in humans. Progr Neurobiol 47: 533–544
Sternad D, Collins D, Turvey MT (1995) The detuning factor in the dynamics of interlimb coordination. Biol Cybern 73: 27–35
Sternad D, Amazeen EL, Turvey MT (1996) Diffusive, synaptic, and synergetic coupling: an evaluation through in-phase and antiphase rhythmic movements. J Mot Behav 28: 255–269
Swinnen SP, Dounskaia N, Verschueren S, Serrien DJ, Daelman A (1995) Relative phase destabilization during interlimb coordination: the disruptive role of kinesthetic afferences induced by passive movement. Exp Brain Res 105: 439–454
Tanji J, Okano K, Sato KC (1988) Neuronal activity in cortical motor areas related to ipsilateral, contralateral and bilateral digit movements of the monkey. J Neurophysiol 60: 325–343
Tax AAM, van der Gon JJD, Gielen CCAM, van der Tempel CMM (1989) Differences in the activation of m. biceps brachii in the control of slow isotonic movements and isometric contractions. Exp Brain Res 76: 55–63
Tax, AAM, van der Gon JJD, Gielen CCAM, Kleyne M (1990) Differences in central control of m. biceps brachii in movement tasks and force tasks. Exp Brain Res 79: 138–142
Teasdale N, Bard C, Fleury M, Paillard J, Forget R, Lamarre Y (1994) Bimanual interference in a deafferented patient and control subjects. In: Swinnen S, Heuer H, Massion J, Casaer P (eds) Interlimb coordination: neural, dynamical, and cognitive constraints. Academic Press, San Diego, pp 243–258
Tuller B, Kelso JAS (1989) Environmentally-specified patterns of movement coordination in normal and split-brain subjects. Exp Brain Res 75: 306–316
Van Bolhuis BM, Medendorp WP, Gielen CCAM (1997) Motor unit firing behavior in human arm flexor muscles during sinusoidal isometric contractions and movements. Exp Brain Res 117: 120–130
Von Holst E (1938) Relative coordination in mammals and man (in German). Pflügers Arch 240: 44–59
Weiller C, Jüptner M, Fellows S, Rijntjes M, Leonhardt G, Kiebel S, Müller S, Diener HC, Thilmann AF (1996) Brain representation of active and passive movements. Neuroimage 4: 105–110
Walter CB, Swinnen SP (1990) Kinetic attraction during bimanual coordination. J Mot Behav 22: 451–473
Wiesendanger M, Wicki U, Rouiller E (1994) Are there unifying structures in the brain responsible for interlimb coordination? In: Swinnen S, Heuer H, Massion J, Casaer P (eds) Interlimb coordination: neural, dynamical, and cognitive constraints. Academic Press, San Diego, pp 179–207
Wimmers RH, Beek PJ, Van Wieringen PCW (1992) Phase transitions in rhythmic tracking movements: a case of unilateral coupling. Hum Mov Sci 11: 217–226
Zanone PG, Kelso JAS (1992) The evolution of behavioral attractors with learning: nonequilibrium phase transitions. J Exp Psychol Hum Percept Perform 18: 403–421